

The fish zonation of the Itanhaém river basin in the Atlantic Forest of southeast Brazil

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Abstract The distribution range of fishes along an upstream–downstream gradient within a river basin is determined by the ecological requirements of each fish species. This differential pattern of distribution may suggest the occurrence of fish zones, where different functional guilds would prevail. The earliest concept of fish zonation highlighted the preferential position of several species in European rivers. Nowadays, there is a consensus that for a broad application of this concept, it is necessary to consider the division in functional groups along the downstream profile as related to reproductive, feed and population dynamics traits. However, for a number of tropical systems, such information does not exist. In this case, it is possible to use the fish family as a surrogate metric, by assuming that it fully covers common aspects of morphology, feeding, and behavior. Using this surrogate metric, we analyzed the distribution range of fish species along an elevation

gradient in a typical Atlantic Forest basin in southeast Brazil. Our objective was to delimit fish zones based on the representativeness of some dominant fish families. Between 2006 and 2008, we sampled 42 sites from the estuary to the headwater creeks in elevations that varied from 3 to 783 m. The data were explored using the species (or family) occurrence, relative numerical abundance (N'), relative biomass (B'), and the importance index (IP). We applied the non-metric multidimensional scaling (NMDS) to ordinate the sampling sites using the Jaccard distance calculated on the species occurrence matrix. Data on family importance were superimposed to the NMDS to check how the distribution and the abundance of the families were correlated to the ordination. We caught 64 species distributed among 25 fish families. Based on the dominance of some families, we propose that the fish assemblage in the Itanhaém river basin can be organized in four fish zones (FZ) and three transitory zones (TZ), which replace each other along the longitudinal gradient. The marine/estuarine fishes dominated in FZ1 and TZ1. The freshwater fishes were dominated by Characidae (FZ2), Heptapteridae (FZ3), and Gymnotidae (FZ4). TZ2 was equally dominated by Characidae, Loricariidae, and Heptapteridae. The distinct assemblage composition along the FZ's may relate to complex interactions involving seasonal patterns of variation in salinity levels (next to estuary), slope, presence of downstream barriers, and availability of food resources. We expect that the patterns observed in

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our study will also be presented in other coastal Atlantic Forest basins in Southeast Brazil.

Keywords East basin · Elevation profile · Species turnover · Freshwater fish families · Functional guilds

Introduction

In order to understand how the river ecosystems are affected by human activities, we need to know how they function in the absence of these activities, i.e., we have to develop reference models for the functioning of these systems (Poff et al., 1997; USEPA, 2002, 2006; Whol & Merritts, 2007). Vannote et al. (1980) were the first to organize the riverine functioning into a comprehensive framework (The River Continuum Concept—RCC), which describes expected patterns and processes along the longitudinal gradient. In the RCC model, the faunal composition and function in a given position are expected to conform to the mean state of the geomorphic and fluvial characteristics of the system. Although several contributions emphasized other external influences, such as the effects of the geomorphology, climate, presence of tributaries, riparian vegetation, and channel discontinuities (Minshall et al., 1983, 1985; Ward & Stanford, 1983, Osborne and Wiley, 1992), the RCC model still remains valuable in predicting the main patterns and processes along the longitudinal gradient in a river (Winemiller & Leslie, 1992; Petry & Schulz, 2006). Concerning the biological aspects, the RCC model predicts that changes in the prevalence of different functional groups along the river position will follow the distribution of the hydrogeomorphic patches (Thorp et al., 2006). For fish communities, a ubiquitous consequence of the RCC concept is that changes in the structural condition promote a shift in the fish groups along the downstream profile. This observation leads to the development of the fish zonation concept, a schematic arrangement of discrete zones, where fish species share similar habitat preferences (Huet, 1959). This concept was first developed for temperate European waters, where the entire river course was divided into five basic zones (*sensu* Aarts & Nienhuis, 2003) following the downstream direction. The need to develop effective tools for assessing river conditions and measure the effects of anthropogenic impacts over

large areas or ecoregions highlights an obvious problem for the application of Huet's fish zonation. For example, Huet's fish zonation does not account for natural differences in species composition among basins, nor it explains which resources are essential for the conservation of each fish zone. Nowadays, it is a consensus that the concept of fish zonation should group species not by their taxonomic status, but by their functional roles in the environment, that is, it must consider their habitat requirements for spawning, nursery, and feeding, their tolerance to non-natural modifications in the river flow and structure, in the water chemistry, and the main aspects of population dynamics relating to longevity, mobility, and growth rates (Aarts & Nienhuis, 2003; Welcomme et al., 2006; Beier et al., 2007; Lasne et al., 2007; Noble et al., 2007; Pont et al., 2007).

The concept of functional groups is related to the concept of ecological guild (Simberloff & Dayan, 1991), as it refers to species that use similar resources and affect the system in similar ways (Higgins & Strauss, 2008). The practical issue with this classification is that it creates effective tools for assessing the ecological integrity of lotic systems. For the fish community, the traditional classification of functional groups follows measurable features related to trophic category (e.g., herbivore, piscivore, and invertivore), population dynamics (e.g., opportunistic, periodic, and equilibrium species), and feeding behaviors (e.g., benthic detritivores, surface feeders, benthic pickers) (Matthews, 1998; Winemiller, 1992, 1996; Winemiller & Rose, 1993; Hoeinghaus et al., 2007; Higgins & Strauss, 2008). Migratory movements, reproductive strategies, longevity, habitats requirements, and tolerance to non-natural degradation can be added to form these functional groups (Karr, 1981; Welcomme et al., 2006; Noble et al., 2007). For instance, Balon (1975) proposed a traditional classification of reproductive fish guilds considering spawning habits and habitats. This classification is used worldwide with minor modifications (Vriese et al., 1994; Aarts & Nienhuis, 2003). Most attempts to create functional fish groups were made in temperate regions of North America and Europe, where biological information is available for several species. However, there is a necessity for developing similar classifications for tropical and sub-tropical systems, as these systems are suffering drastic changes in their flow regime around the

catchments basins caused by water abstraction, damming, agriculture, and urbanization (Welcomme et al., 2006).

Unfortunately, there is a lack of information about the ecology of most species in tropical streams and rivers. In order to help developing similar classification in tropical regions, a “fish environmental guild” arrangement was recently proposed to assist in constructing reference conditions for assessing the response of the fish biota to changes in the system’s flow and geomorphology (Welcomme et al., 2006). The foundation for identifying these environmental guilds is based on the species-specific preference for a given river location, which highlights the importance of the longitudinal distribution of fish species in riverine ecosystems worldwide (Kadye et al., 2008; Araújo et al., 2009; Orrego et al., 2009). In this protocol, the species were organized in zones according to its upstream–downstream occurrence (Rhithron, Potamon, and Estuary). In the rhithron zones, there is a prevalence of resident and small-bodied fishes that can be divided in sub-groups according to their preferences for fast flowing and steep stretches (riffle guild) or for slower flowing and lower gradient areas (pool guild) (Schlosser, 1982; Angermeier & Karr, 1983; Buhrnheim & Fernandes, 2003; Langeani et al., 2005). Downstream, the potamonic zones are inhabited by lentic species distributed in habitats such as the main channels, connected or eventually disconnected lagoons, inundated floodplain, backwaters, and the floodable forests or the riparian vegetation. The potamonic guilds presents more complex and diversified ecological traits related to various levels of resistance to anoxia or to specific reproductive behaviors. The Estuarine guilds are distinguished by their response to daily or seasonal changes in salinity levels. Feeding categories present complex relationships with body size, river location, morphological restrictions, and ontogenetic changes and, thus, were not included in the environmental fish guilds (Welcomme et al., 2006). As a general pattern, it appears that strict top-carnivores (piscivorous) are rare and restricted to fishes with a large body size. As a consequence, top-carnivores are restricted to the lower basin portions such as the estuary and the potamon zones, decreasing upstream when the dimension of the aquatic habitats became too reduced to support larger fishes (Gilliam et al., 1993; Petry & Schulz, 2006). However, the carnivorous habit can be

found from the estuary to the rhithron zones, and includes species that feed on a wide range of organisms, depending on their longitudinal distribution pattern in the river basin.

Despite obvious taxonomic differences among the species used for the propositions of the European fish zonation (Huet, 1959) and the species considered in the “fish environmental guilds” (Welcomme et al., 2006), both arrangements highlighted the preference of some species for lotic and fast flowing waters upstream or for lentic habitats downstream, and the salinity influence’s next to the estuaries, i.e., they describe aspects of the overall influence of the longitudinal gradient in riverine ecosystems. Lamouroux et al. (2002) evaluated intercontinental convergence in fish traits along a longitudinal profile in temperate streams of Europe and North America. They found significant and similar response of body size, fecundity, maximum age, shape factor, and the preference for vertical position in the channel. While the first three responses were probably due to intercorrelated allometric effects (Woodward et al., 2005), the last two responses expressed the preference for pool habitats and the use of water column in downstream reaches, and the preference for fast flowing, shallow reaches, and for benthic habits in upstream portions.

In this article, we evaluated the fish assemblage structure and composition along an altitudinal range in the Itanhaém river basin, the second largest coastal basin of the São Paulo State. This basin is part of the East Basin system (Menezes, 1972), which extends for more than 2,000 km along the Brazilian coast line, amidst the remainder of the Atlantic Forest, one of the most threatened biomes in the country and a world hotspot of species biodiversity (Myers et al., 2000). The East basin is composed by a number of short and isolated drainages, which flows directly to the Atlantic Ocean, promoting high levels of endemism (Menezes, 1972). In Southeast Brazil, between the States of São Paulo and Santa Catarina, the geomorphology of the coastal drainages is strongly influenced by the Serra do Mar mountain range. This mountain formation is the border of an interior low-relief plateau of Pre-Cambrian origin that isolates the high stretches (above 700 m) from the lower coastal plain region (below 50 m), a geologic formation covered by soil deposits of Quaternary age (Almeida & Carneiro, 1998). Owing to this geomorphology, the

coastal fish fauna of São Paulo State is primarily divided into three distinct groups, concerning evolutionary and biogeographical histories: (i) a marine/estuarine group, (ii) a freshwater group occurring at low/moderate elevations in freshwater coastal plain and in the mountain range, and (iii) a fish group occurring above 600/700 m, at the headwaters of the low-relief areas in the plateau next to the drainages limits (Leung & Camargo, 2005; Takako et al., 2005; Oyakawa et al., 2006; Ribeiro, 2006; Ribeiro et al., 2006; Louro, 2007; Menezes et al., 2007; Serra, 2007). Despite the proximity of great metropolitan areas, little is known about the patterns of longitudinal fish zonation that could account for more than biogeographical elements. Thus, by sampling from the estuary to the plateau, we expect to identify changes between these fish groups related to the elevation profile. We analyzed the prevalence of dominant fish species and families throughout the sampling sites and propose a schematic model of fish zonation that can help to understand the ecological processes prevailing along the upstream/downstream gradient.

Materials and methods

Study area

The Brazilian coastal drainages of eastern continental margin were originated at Triassic from the break-up of Gondwana (Ribeiro, 2006). The Itanhaém river basin (23°35'; 24°15' S and 46°35'; 47°00' W) has 930 km² and can be divided into four regions according to its altitude, declivity, and geomorphology (Camargo et al., 1997). Although the superior region (the plateau) is located around the most populated city in Brazil (São Paulo), it is inside of two environmental protection areas, the “Parque Estadual da Serra do Mar (PESM)” and the “Área de Proteção Ambiental (APA) Capivari-Monos.” These protection areas sustain well preserved remnants of the original Atlantic Rain Forest. Between 700 and 50 m there is a steep region of mountain range (the Serra do Mar) that is still inserted in the PESH. The coastal plain, a low-relief region formed by Quaternary deposits, is mostly covered by the restinga vegetation, an herbaceous–arbusive lowland forest that is partly affected by anthropogenic

pressures as agriculture (mostly banana plantation) and urbanization. The lower region of the basin is covered by mangrove vegetation surrounding the river channels, and is largely affected by uncontrolled urbanization and sewage discharge (Camargo et al., 1997; Nogueira, 2001; Pereira, 2002).

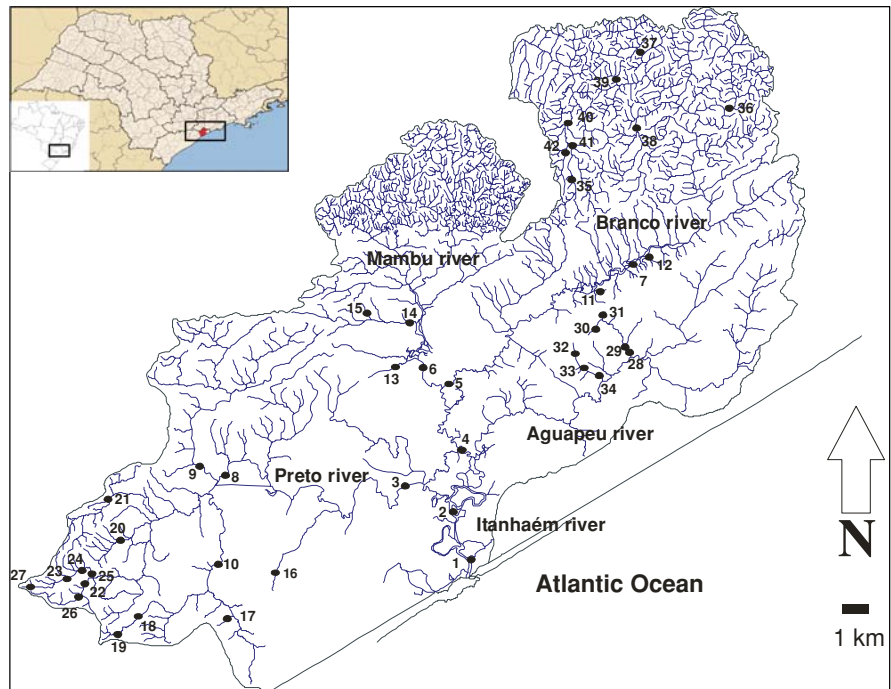
Hydrography

Four main rivers (Branco, Mambu, Preto, and Aguapeu) form the Itanhaém river channel. The Branco and Mambu microbasins originate in the plateau and rapidly reach the coastal plain after passing throughout short and steep valleys in the Serra do Mar. The Mambu River crosses a low-relief stretch in the coastal plain and joins the Branco River. The Aguapeu headwaters originate at 400 m in the Serra do Bariri, a mountain formation between Branco and Aguapeu microbasins. Its main channel presents dark waters and low levels of dissolved oxygen and pH. Almost all the original restinga vegetation in its surroundings was replaced by agriculture or urban areas. The Preto microbasin originates at three different areas. The majority of its headwaters are above 700 m in a well-preserved region inside the PESH. Other headwater streams originate at 400 m in an area partially occupied by agriculture, known as Serra dos Itatins. The last stream system originates at low elevations inside the last preserved remnants of the restinga forest in the region. It differed from the other headwaters by its dark waters, high acidity, and low levels of oxygen (similar to the Aguapeú River). The Preto and Branco main channels form the Itanhaém River, a sixth-order estuarine channel 7 km long, 100–200 m wide, and 1–4 m deep (Fig. 1).

Fish sampling

The fishes were sampled between 2006 and 2008 in 42 sites, from estuary to plateau headwaters, with the use of different sampling techniques. The estuary and the main river channels (larger than 10 m width) were fished with ten series of gillnets (20 m × 1.0 m and mesh sizes ranging from 3 to 12 cm between opposed knots), a sieve (1.5 m × 1.0 m, with 2-mm mesh size), and two pairs of funnel traps. Streams and creeks were sampled by electric fishing using an electric generator (Yamaha, model EF2600, 2.3 kVA,

Fig. 1 Location and hydrography of the Itanhaém river basin with the 42 sampling sites



60 Hz) linked to a current rectifier in wider channels or a backpack (Smith-root, model LR-24) in less accessible reaches. Both equipments were used with direct current at 600 V. Fish effort was standardized to 12 h for gillnets and funnel traps (late afternoon to next morning), and ten sweeps of the sieve in the river margins. Electric fishing was carried out by two persons passing once against the current. The length of the segments varied between 50 and 100 m due to the difficulty of access in some stretches. Twenty sites ranging from 0 to 130 m high were repeatedly sampled in February, May, August, and November of 2006. In November of 2007, eight streams above 700 m were sampled once. Additional 14 streams, from altitudes ranging from 8 to 263 m, were sampled in March 2008 (Fig. 1; Table 1).

On collection, all fishes were immediately fixed in 10% formalin for later identification, and weighed (g). Some specimens were taken to the Museu de Zoologia da Universidade de São Paulo (MZUSP) for taxonomic identification and for deposition of voucher specimens.

Data analysis

Owing to the inherent bias resulting from the use of different sampling techniques, the data were explored

using species occurrence, relative numerical abundance ($N'_{ij} = N_{ij}/N_j$), relative biomass ($B'_{ij} = B_{ij}/B_j$) and the importance index calculated at species and family levels. The *IP* index was quantified as: $IP_{ij} = N_{ij} * B_{ij} / \sum (N_{ij} * B_{ij})$, which is a modification of the Ponderal index originally described by Beaumord and Petrere Jr. (1994). The original Ponderal index was expressed in percentage, while here the *IP* index ranged from 0 to 1, as for the values of N'_{ij} and B'_{ij} . N_{ij} and B_{ij} are, respectively, the number of individuals and biomass of species (or family) *i* in sample *j*, and N_j and B_j are, respectively, the totals for sample *j*. N'_{ij} , B'_{ij} and IP_{ij} measures the representativeness of each species (or family) in local samples as relative contributions. These procedures allow a minimization of the effects of consistent bias resulting from the sampling effect. Some sites were sampled more frequently than others (Table 1), and so we combined temporal collections within a site using the mean values of N'_{ij} , B'_{ij} and IP_{ij} (Winemiller & Leslie, 1992; Lasne et al., 2007). The spatial turnover was explored with the non-metric multidimensional scaling (NMDS) using the Jaccard distance on the species occurrence matrix (Ludwig & Reynolds, 1988). The *IP* index matrix at the family level was superimposed to this ordination using the “envfit” function from Vegan package to check how

Table 1 Location and main characteristics of the sampling sites

Site	Geographic coordinates	Location	River type	Microbasin	Proposed fish or transition zones	Distance from the Itanhaém river mouth (km)	Elevation (m)	River order	Width (m)	Depth (m)	Number of samples	Sampling technique	Species richness	N_t	W_t (g)
1	46W 47'56" 24S 10'41"	Coastal plain	Estuarine channel	Itanhaém	FZ1	2.33	3	6	200	2.50	4	gn, si, ft	13	40	2527.85
2	46W 48'15" 24S 9'21"	Coastal plain	Estuarine channel	Itanhaém	TZ1	5.24	4	6	100	3.10	4	gn, si, ft	10	67	4040.47
3	46W 49'01" 24S 08'32"	Coastal plain	Black water	Preto	TZ1	8.22	4	5	40	3.00	4	gn, si, ft	12	14	342.80
4	46W 47'40" 24S 07'27"	Coastal plain	White water	Branco	TZ1	11.93	5	5	200	2.00	4	gn, si, ft	8	41	1265.3
5	46W 48'28" 24S 05'4"	Coastal plain	White water	Branco	FZ2	19.26	10	4	30	2.20	3	gn, si, ft	8	27	2438.62
6	46W 49'26" 24S 04'05"	Coastal plain	Clear water	Mambu	FZ2	21.83	10	4	30	1.80	4	gn, si, ft	13	52	565.69
7	46W 43'20" 24S 01'46"	Coastal plain	White water	Branco	FZ2	39.83	18	4	20	2.20	4	gn, si, ft	12	76	1588.98
8	46W 56'32" 24S 07'59"	Coastal plain	Black water	Preto	FZ2	32.8	9	5	15	2.20	4	gn, si, ft	16	99	3117.61
9	46W 57'24" 24S 7'13"	Coastal plain	Clear water	Preto	FZ2	35.9	16	4	25	0.80	4	gn, si, ft	18	150	65820.89
10	46W 56'48" 24S 10'43"	Coastal plain	Black water	Preto	FZ2	38.72	10	3	15	2.10	4	gn, si, ft	12	37	4999.91
11	46W 44'18" 24S 02'38"	Coastal plain	Clear water	Branco	TZ2	33.99	69	1	1.60	0.10	4	ef	8	50	235.99
12	46W 42'20" 24S 01'37"	Coastal plain	Clear water	Branco	TZ2	43.35	58	2	4.80	0.20	4	ef	14	66	830.80
13	46W 49'56" 24S 04'17"	Coastal plain	Clear water	Mambu	FZ2	23.69	19	1	4.70	0.30	4	ef	20	97	426.53
14	46W 49'25" 24S 02'56"	Coastal plain	Clear water	Mambu	FZ2	24.46	14	2	9.70	0.20	4	ef	22	163	707.81
15	46W 50'46" 24S 02'41"	Mountain range	Clear water	Mambu	FZ3	27.11	197	1	Not measured	Not measured	1	ef	3	38	291.62
16	46W 54'43" 24S 11'09"	Coastal plain	Black water	Preto	FZ2	27.99	11	1	4.30	0.20	3	ef	15	379	376.36
17	46W 55'27" 24S 13'30"	Coastal plain	Black water	Preto	FZ2	45.04	17	1	1.30	0.20	3	ef	17	126	433.98

Table 1 continued

Site	Geographic coordinates	Location	River type	Microbasin	Proposed fish or transition zones	Distance from the Itanhaém river mouth (km)	Elevation (m)	River order	Width (m)	Depth (m)	Number of samples	Sampling technique	Species richness	N_t	W_t (g)
18	46W 24S 59'19" 12'11"	Coastal plain	Clear water	Preto	FZ2	44.75	38	2	3.30	0.10	4	ef	16	165	572.23
19	47W 24S 00'01" 12'42"	Mountain range	Clear water	Preto	FZ3	46.28	134	2	4.30	0.10	3	ef	6	43	260.91
20	46W 24S 59'56" 09'49"	Coastal plain	Clear water	Preto	FZ2	40.42	36	3	7.90	0.20	4	ef	19	103	890.65
21	47W 24S 00'22" 08'23"	Coastal plain	Clear water	Preto	TZ2	41.78	60	3	6.80	0.10	4	ef	13	106	536.12
22	47W 24S 01'29" 11'29"	Mountain range	Clear water	Preto	TZ2	45.49	80	3	Not measured	Not measured	1	ef	10	91	244.21
23	47W 24S 01'56" 10'56"	Mountain range	Clear water	Preto	FZ3	46.37	190	2	Not measured	Not measured	1	ef	5	46	216.74
24	47W 24S 01'28" 10'39"	Mountain range	Clear water	Preto	FZ3	45.39	131	3	Not measured	Not measured	1	ef	8	33	118.62
25	47W 24S 00'55" 10'58"	Mountain range	Clear water	Preto	TZ2	44.08	54	3	Not measured	Not measured	1	ef	7	42	235.27
26	47W 24S 01'35" 11'41"	Mountain range	Clear water	Preto	TZ2	45.92	83	2	Not measured	Not measured	1	ef	8	92	197.72
27	47W 24S 02'38" 11'17"	Mountain range	Clear water	Preto	FZ3	47.71	263	2	Not measured	Not measured	1	ef	5	32	192.03
28	46W 24S 42'07" 04'03"	Coastal plain	Clear water	Aguapeu	FZ2	35.11	12	2	Not measured	Not measured	1	ef	8	139	174.78
29	46W 24S 42'08" 04'01"	Coastal plain	Clear water	Aguapeu	FZ2	35.18	11	2	Not measured	Not measured	1	ef	8	143	168.85
30	46W 24S 42'20" 03'23"	Mountain range	Clear water	Aguapeu	TZ2	36.57	50	1	Not measured	Not measured	1	ef	6	101	397.95
31	46W 24S 42'13" 03'7"	Mountain range	Clear water	Aguapeu	TZ2	36.7	75	1	Not measured	Not measured	1	ef	4	22	68.49
32	46W 24S 44'35" 04'48"	Mountain range	Clear water	Aguapeu	TZ2	28.79	67	1	Not measured	Not measured	1	ef	5	40	454.59
33	46W 24S 44'12" 05'06"	Mountain range	Clear water	Aguapeu	FZ2	27.95	27	2	2.20	0.30	1	ef	10	108	675.17
34	46W 24S 43'55" 05'20"	Coastal plain	Clear water	Aguapeu	FZ2	27.24	8	2	7.10	0.35	1	ef	9	87	134.54

Table 1 continued

Site	Geographic coordinates	Location	River type	Microbasin	Proposed fish or transition zones	Distance from the Itanhaém river mouth (km)	Elevation (m)	River order	Width (m)	Depth (m)	Number of samples	Sampling technique	Species richness	N_t	W_t (g)
35	46W 23S 43'46" 59'01"	Pateaul	Clear water	Branco	FZ4	81.41	787	3	5.00	0.20	1	ef	3	94	593.89
36	46W 23S 38'07" 56'15"	Pateaul	Clear water	Branco	FZ4	62.19	732	4	Not measured	Not measured	1	ef	5	55	297.95
37	46W 23S 41'12" 54'18"	Pateaul	Clear water	Branco	FZ4	67.70	746	3	5.70	0.40	1	ef	6	149	457.55
38	46W 23S 41'29" 56'33"	Pateaul	Clear water	Branco	FZ4	64.94	747	4	6.00	0.50	1	ef	3	29	134.91
39	46W 23S 41'43" 55'15"	Pateaul	Clear water	Branco	FZ4	67.02	743	3	2.80	0.30	1	ef	7	70	381.76
40	46W 23S 43'58" 56'37"	Pateaul	Clear water	Branco	FZ4	76.53	760	3	2.25	0.30	1	ef	6	42	236.68
41	46W 23S 43'54" 57'13"	Pateaul	Clear water	Branco	FZ4	77.9	770	3	Not measured	Not measured	1	ef	4	40	171.90
42	46W 23S 43'59" 57'24"	Pateaul	Clear water	Branco	FZ4	78.24	770	2	Not measured	Not measured	1	ef	4	44	114.90

N_t total number of fish collected, W_t total weigh collect

For the sites sampled more than once, N_t and W_t are the average values per sampling

the family importance was related to the sites' ordination (R Development Core Team, 2008). The “envfit” function finds directions in ordination space toward which the vectors change most rapidly having maximal correlations with the configuration (Oksanen et al., 2009). A randomization test (9999 permutations) was used to verify the significance of the importance of each family using the squared correlation coefficient (r^2). The significance level was considered 5% or less. We plotted the *IP* values versus elevation taking into account only the families that comprise 80% of the total importance. In order to detect dependence patterns, the relationships were explored with robust locally weighted regression (LOWESS), a polynomial smoothing algorithm (R Development Core Team, 2008). The same procedure was carried out for relative numeric abundance and relative biomass.

Results

Owing to the easiness of access, 70% of the samples were collected below an altitude of 100 m. The main river channels ranged from elevations of 3–18 m while the streams and creeks ranged from 8 to 787 m. We had no access to streams between 300 and 700 m located in the steep portion of the Serra do Mar mountain range. The lowest streams are in the Preto (site 16) and Aguapeu (sites 28, 29, and 34) microbasins. The highest main channels were at 16 (site 9) and 18 m (site 7) next to the Serra do Mar foothills. The distances to the basin mouth ranged from 2.33 km (in site 1) to 78.24 km in site 42. Five black-water sites were sampled in the Preto microbasin, two with electrofisher, and three with gillnets, funnel traps, and sieve (Table 1).

The species richness totaled 64, distributed in 25 fish families, 3,438 individual and approximately 98 kg. Nineteen species and 12 families were marine/estuarine, with Ariidae and Sciaenidae being the most abundant. Overall, the marine/estuarine families had low representativeness (3.61% of the numeric abundance and 7.16% of the total weight) due to the low number of estuarine environments sampled. The freshwater families Characidae, Heptapteridae, Gymnotidae, and Loricariidae account for 66% of the numeric abundance and 80% of the total weight. If measured by the *IP* index, these families accounted

for 78.36% of the total importance. Erythrinidae, represented by the piscivorous *Hoplias malabaricus* (Block, 1794), was the fifth most important family. Six freshwater species occurred exclusively at the plateau sites, while 39 were exclusively caught between 4 and 263 m in the coastal plain or in the mountain range sites. The freshwater species *Geophagus* cf. *brasiliensis* (Quoy & Gaimard, 1824), *H. malabaricus*, *Phalloceros* spp., and *Gymnotus pantherinus* (Steindachner, 1908) occurred from the coastal plain to the plateau. The conservation status of four species was officially ranked as endangered or vulnerable according to Machado et al. (2005). They were captured exclusively in the black-water streams or in the highest plateau sites. One introduced species the “Pacu” *Piaractus mesopotamicus* (Holmberg, 1887) was captured in site 4 (Table 2).

The number of individuals tended to be higher in the electrofished sites whereas the sites sampled with gillnets, funnel traps, and sieve yielded higher fish weigh, which can be partly assigned to the sampling effect (Table 1). As expected, the sampling technique was responsible for the main source of variability, which was expressed by the first ordination axis (Fig. 2). The electrofished sites (streams and creeks) were in the right side of Fig. 2a, and the main river channels in the left. The two estuarine sites (open triangles) were in the left side of the dimension 1 while the plateau is in the lower right side (Fig. 2a). Considering only the freshwater sites below 300 m, the spatial species turnover expressed by dimension 1 was linearly correlated with the log of elevation ($r = 0.89$; $P < 0.01$; $n = 32$) (Fig. 2b). The *IP* index of six marine/estuarine families (Paralichthyidae, Ephippidae, Carangidae, Ariidae, Tetraodontidae, and Sciaenidae) was significantly associated to the ordination ($P \leq 0.05$, Fig. 2a). Except for Sciaenidae and Ariidae, all the families were represented by one or two individuals caught exclusively in site 1. For the freshwater families, we detected significant association between Gymnotidae, and the plateau sites, where 84% of the individuals were caught. The importance of Characidae, Heptapteridae, and Loricariidae were associated to the coastal plain and to the mountain range sites below 300 m (Fig. 2a). However, we found that Characidae and Heptapteridae presented opposite patterns of importance. The Characidae was better represented below 40 m, while Heptapteridae became the dominant family above

Table 2 Number of individuals (N), biomass (W, in grams), and IP index ($\times 100$) for species captured in the proposed fish zones

Species	Family	FZ1 (1)			TZ1 (3)			FZ2 (16)			TZ2 (9)			FZ3 (5)			FZ4 (8)		
		N	W	IP $\times 100$	N	W	IP $\times 100$	N	W	IP $\times 100$	N	W	IP $\times 100$	N	W	IP $\times 100$	N	W	IP $\times 100$
<i>Catharops spixii</i> (Agassiz, 1829)*	Ariidae	20	1286.51	84.60	5	584.55	3.14												
<i>Genidens genidens</i> (Valenciennes, 1840)*	Ariidae	5	744.32	12.24	6	904.78	5.83												
<i>Bairdiella ronchus</i> (Cuvier, 1830)*	Sciaenidae	3	191.47	1.89	38	1949.73	79.63												
<i>Micropogonias furnieri</i> (Desmarest, 1823)*	Sciaenidae	2	63.12	0.42	6	175.20	1.13												
<i>Eucinostomus melanopterus</i> (Bleeker, 1863)*	Gerreidae	2	18.71	0.12	2	64.83	0.14												
<i>Centropomus parallelus</i> Poey, 1860*	Centropomidae	1	121.19	0.40	1	10.42	0.01	2	34.98	<0.01									
<i>Caranx cf. latus</i> Agassiz, 1831*	Carangidae	1	12.66	0.04															
<i>Chaetodipterus faber</i> (Broussonet, 1782)*	Ephippidae	1	9.86	0.03															
<i>Diapterus rhombeus</i> (Valenciennes, 1830)*	Gerreidae	1	7.53	0.02															
<i>Etropus</i> sp.*	Paralichthyidae	1	5.31	0.02															
<i>Lagocephalus laevigatus</i> (Linnaeus, 1758)*	Tetraodontidae	1	30.55	0.10															
<i>Menticirrhus americanus</i> (Linnaeus, 1758)*	Sciaenidae	1	13.53	0.04															
<i>Sphaeroides spengleri</i> (Bloch, 1785)*	Tetraodontidae	1	23.11	0.08															
<i>Deuterodon iguape</i> Eigenmann, 1907	Characidae	28	43.15	1.30	451	3232.39	43.92	114	798.42	31.80									
<i>Geophagus cf. brasiliensis</i> (Quoy & Gaimard, 1824)	Cichlidae	8	330.76	2.84	48	1934.27	2.80	3	35.84	0.04	1	4.43	0.01	6	147.62	0.20			
<i>Lycengraulis grossidens</i> (Agassiz, 1829)*	Engaulidae	5	90.05	0.48															
<i>Hoplias malabaricus</i> (Bloch, 1974)	Erythrinidae	4	720.28	3.10	29	6403.06	5.59							1	7.20	<0.01			

Table 2 continued

Species	Family	FZ1 (1)			TZ1 (3)			FZ2 (16)			TZ2 (9)			FZ3 (5)			FZ4 (8)		
		N	W		IP × 100	N	W	IP × 100	N	W	IP × 100	N	W	IP × 100	N	W	IP × 100	N	W
<i>Oligosarcus hepsetus</i> (Cuvier, 1829)	Characidae					4	88.89	0.38	21	64505.48	40.81	1	0.62	<0.01					
<i>Stellifer rastriifer</i> (Jordan, 1889)*	Sciaenidae					4	223.94	0.96											
<i>Hoplosternum littorale</i> (Hancock, 1828)	Callichthyidae					3	192.47	0.62	3	540.28	0.05								
<i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)	Heptapteridae					2	128.83	0.28	25	2664.69	2.01	4	249.14	0.35					
<i>Phalloceros</i> spp.	Poeciliidae					1	0.18	<0.01	146	283.10	1.25	80	75.50	2.11	25	13.06	0.43	220	71.18
<i>Characidium</i> spp.	Crenuchidae					1	0.10	<0.01	113	75.54	0.26	29	23.62	0.24					3.54
<i>Rineloricaria kronei</i> (Miranda Ribeiro, 1911)	Loricariidae					1	23.61	0.03	48	307.21	0.44	10	51.57	0.18	1	0.81	<0.01		
<i>Crenicichla lacustris</i> (Castelnau, 1856)	Cichlidae					1	38.67	0.04	12	222.55	0.08	2	30.57	0.02					
<i>Glanidium melanopterum</i> Miranda Ribeiro, 1918	Auchenipteridae					1	18.92	0.02	3	170.97	0.02								
<i>Piaractus mesopotamicus</i> (Holmberg, 1887) [▲]	Characidae					1	59.25	0.06											
<i>Minagoniates microlepis</i> (Steindachner, 1877)	Characidae								247	83.85	0.62	12	13.96	0.06					
<i>Minagoniates lateralis</i> (Nichols, 1913) [●]	Characidae								180	53.53	0.29								
<i>Kronichthys heylandi</i> (Boulenger, 1900)	Loricariidae								106	252.69	0.81	138	421.09	20.30	20	54.11	1.42		
<i>Scleromystax macropterus</i> Regan, 1913 [●]	Callichthyidae								67	51.81	0.10								
<i>Hyphessobrycon reticulatus</i> Ellis, 1911	Characidae								64	104.07	0.20								
<i>Scleromystax barbatus</i> (Quoy & Gaimard, 1824)	Callichthyidae								50	106.22	0.16	38	68.63	0.91					

Table 2 continued

Species	Family	FZ1 (1)			TZ1 (3)			FZ2 (16)			TZ2 (9)			FZ3 (5)			FZ4 (8)		
		N	W	IP	N	W	IP	N	W	IP	N	W	IP	N	W	IP	N	W	IP
<i>Acentronichthys leptos</i> Eigenmann & Eigenmann, 1889	Heptapteridae	40		27.66	0.03	4	10.60	0.01											
<i>Pseudotothyris obtusa</i> (Miranda Ribeiro, 1911)	Loricariidae	35		12.72	0.01														
<i>Pimelodella</i> cf. <i>transitoria</i> Miranda Ribeiro, 1905	Heptapteridae	26		155.28	0.12	4	33.63	0.05											
<i>Gymnotus pantherinus</i> (Steindachner, 1908)	Gymnotidae	21		210.78	0.13	6	102.88	0.22	2	15.07	0.04						216	1956.46	95.55
<i>Rhamdioglanis</i> cf. <i>transfasciatus</i> Miranda Ribeiro, 1908	Heptapteridae	19		186.57	0.11	91	1305.27	41.49	81	894.37	95.01								
<i>Hollandichthys multifasciatus</i> (Eigenmann & Norris, 1900)	Characidae	16		81.43	0.04	16	105.95	0.59											
<i>Schizolecithichthys guntheri</i> (Miranda Ribeiro, 1918)	Loricariidae	13		3.66	<0.01	77	26.19	0.70	21	9.58	0.26								
<i>Callichthys callichthys</i> (Linnaeus, 1758)	Callichthyidae	10		92.20	0.03														
<i>Rivulus santensis</i> Köhler, 1906	Rivulidae	8		3.85	<0.01														
<i>Bryconamericus</i> cf. <i>microcephalus</i> Miranda Ribeiro, 1908	Characidae	7		14.35	<0.01	9	11.02	0.03											
<i>Gymnotus</i> cf. <i>carapo</i> Linnaeus, 1758	Gymnotidae	10		320.16	0.10														
<i>Ancistrus</i> sp.	Loricariidae	6		19.75	<0.01	11	50.75	0.20	1	5.29	0.01								
<i>Trichomycterus</i> cf. <i>zonatus</i> (Eigenmann, 1918)	Trichomycteridae	5		5.93	<0.01	18	31.01	0.20	10	16.89	0.22								
<i>Nannostomus</i> cf. <i>beckfordi</i> Günther, 1872 ^a	Lebiasinidae	5		0.90	<0.01														

Table 2 continued

Species	Family	FZ1 (1)			TZ1 (3)			FZ2 (16)			TZ2 (9)			FZ3 (5)			FZ4 (8)		
		N	W	IP	N	W	IP	N	W	IP	N	W	IP	N	W	IP	N	W	IP
<i>Synbranchus marmoratus</i> Bloch, 1975	Synbranchidae							4	27.24	<0.01	1	87.02	0.03						
<i>Trichomycterus</i> sp2	Trichomycteridae							3	1.92	<0.01	4	5.11	0.01						
<i>Characidium</i> sp1	Crenuchidae							2	4.52	<0.01	28	42.50	0.42	30	66.31	2.61			
<i>Awatous tajasica</i> (Lichtenstein, 1922)*	Gobiidae							2	11.13	<0.01	5	26.69	0.05						
<i>Rineloricaria</i> sp1	Loricariidae							2	12.96	<0.01									
<i>Trichomycterus</i> sp1	Trichomycteridae							1	0.46	<0.01	1	1.97	<0.01						
<i>Asynanax janeiroensis</i> Eigenmann, 1908	Characidae							1	36.72	<0.01									
<i>Centropomus undecimalis</i> (Bloch, 1796)*	Centropomidae							1	158.32	<0.01									
<i>Eugerres brasiliatus</i> (Valenciennes, 1830)*	Gerreidae							1	147.51	<0.01									
<i>Mugil curema</i> Valenciennes, 1836*	Mugilidae							1	103.41	<0.01									
<i>Rineloricaria</i> aff. <i>latirostris</i> (Boulenger, 1900)■	Loricariidae										1	18.18	0.01						
<i>Pseudotocinclus</i> cf. <i>tietensis</i> (R. Ihering, 1907)†	Loricariidae													28	41.13	0.26			
<i>Characidium</i> sp2	Crenuchidae													14	20.51	0.06			
<i>Trichomycterus</i> sp3	Trichomycteridae													13	45.11	0.13			
<i>Hypostomus</i> sp.	Loricariidae													12	61.02	0.17			
<i>Asryanax</i> sp.	Characidae													10	34.56	0.08			
<i>Glandulocauda melanogenys</i> Eigenmann, 1911†	Characidae													3	4.75	<0.01			
Total species richness		13			20			42			26			10			10		
Total number of individuals		40			122			1854			707			192			523		

Table 2 continued

Species	FZ1 (1)		TZ1 (3)		FZ2 (16)		TZ2 (9)		FZ3 (5)		FZ4 (8)	
	N	W	N	W	N	W	N	W	N	W	N	W
Total weight (g)	13		20		42		26		10		10	

* Marine/Estuarine species. [▲] Introduced species. [#] Conservation status officially ranked as vulnerable or endangered (Machado et al. 2005). [●] Species found only in acidic black-water streams between the States of São Paulo and Santa Catarina (Menezes et al. 2007). [■] Needs taxonomic confirmation because *R. latirostris* does not occur in the East basin. ^Δ The species is known for the Esquibo river (Guyana), and the middle and lower Amazon. Its presence in some drainages of the East Basin is probably due to introduction by aquarists, but until now there is no consensus about this fact. Furthermore, the species needs a broadly taxonomic revision throughout its distribution range (Menezes et al. 2007; Britski, personal communication). The *IP* index was multiplied by 100 to facilitate the comparisons among the less important species. After FZ and TZ, the number between parentheses refers to the number of sites sampled in each zone

100 m. Loricariidae showed a modal distribution with a peak between 40 and 100 m. It reached the highest *IP* value at site 31 (75 m high, *IP* = 0.72) coinciding with the absence of Characidae and with the low importance of Heptapteridae (*IP* = 0.25). Gymnotidae became dominant above 700 m, where the contribution of the other three families was negligible. The patterns described by the *IP* index followed similar trends when we considered the relative numerical abundance or relative biomass (Fig. 3).

Species zonation

With the proposed fish zonation we attempted to organize the main fish groups along the longitudinal gradient in the Itanhaém river basin. The main characteristics of the fish zones (FZ's) and the related sites were summarized in Tables 1 and 2, and Fig. 4. The lowest site sampled with the eletrofischer (site 34 at 8 m) and the highest site sampled with gillnets, sieves, and funnel traps (site 7 at 18 m) were inside the limits of FZ2 (Table 1). So, it appears that the sampling effects did not influence the delimitation of the FZ's and the TZ's. The estuarine portion formed the first zone (FZ1), which was inhabited only by marine/estuarine species. Most species of this zone have their spatial distribution limited by the ranges of the saline level, which is, in turn, influenced by the tidal regime and by the amount of freshwater flowing from the upper basin portions. In our sample, FZ1 was characterized by site 1 in the Itanhaém river channel. Louro (2007) caught 54 marine/estuarine species in the same area but we caught only 18 which probably indicates a low sampling efficiency for the estuarine habitats. The most representative species were the Ariidae catfishes *Catorops spixii* (Agassiz, 1829) (*IP* = 84.60) and *Genidens genidens* (Valenciennes, 1840) (*IP* = 12.24). Above FZ1 there was a reduction in the richness of marine species, and the appearance of some freshwater species. We defined this region as the transition zone (TZ1) between the estuarine and the freshwater environments. In TZ1 we caught 20 species, being only eight of marine/estuarine origin. The dominant species was the Sciaenidae *Bairdiella ronchus* (Cuvier, 1830) (*IP* = 79.63). The 14 freshwater species summed only 10% of the total importance. TZ1 was characterized by sites 2 to 4. The second fish zone (FZ2)

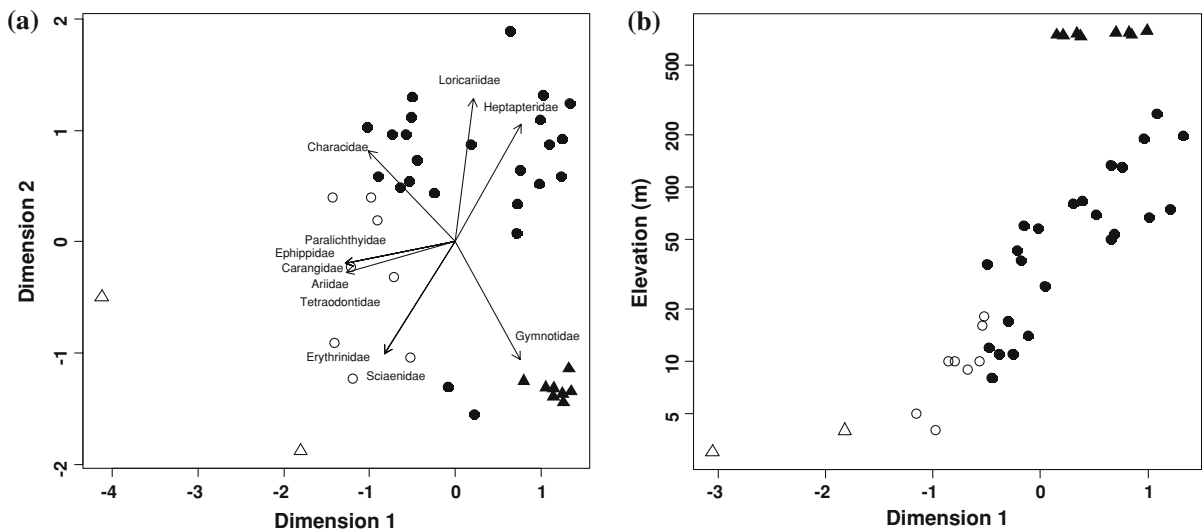


Fig. 2 **a** Two-dimensional NMDS ordination of the sampling sites using the Jaccard distance on the species occurrence matrix. The *IP* index matrix at the family level was superimposed to this ordination using the “envfit” function from Vegan package to check how the family importance was related to the sites’ ordination. Only the families significantly

associated to the ordination ($P \leq 0.05$) were plotted. Stress = 0.1256. **b** Scatterplot of elevation versus dimension 1. Elevation is in natural logarithmic scale. *Open triangles* estuarine sites, *open circles* main rivers channels in the coastal plain, *black circles* streams in the coastal plain and mountain range, *black triangles* plateau headwater streams

was characterized by 16 sampling sites below 40 m high (freshwater main channels and streams). From the 42 species, only four were from marine/estuarine environments: the Centropomidae *Centropomus parallelus* Poey, 1860 and *C. undecimalis* (Bloch, 1796), the Gerreidae *Eugerres brasiliensis* (Valenciennes, 1830), the Mugilidae *Mugil curema* Valenciennes, 1836, and the Gobiidae *Awaous tajasica* (Lichtenstein, 1822). Although the saline water does not reach this zone, the water level still depends of the tidal regime and shows daily fluctuations. So, the lower limit of FZ2 cannot be defined by a constant elevation. The dominant species were the Characidae *Deuterodon iguape* Eigenmann, 1907 ($IP = 43.92$) and *Oligosarcus hepsetus* (Cuvier, 1829) ($IP = 40.81$). Nine sites between 40 and 100 m represented the second transition zone (TZ2) with 20 species. TZ2 was dominated by the Characidae *D. iguape* ($IP = 31.80$), the Heptapteridae *Rhamdioglanis* cf. *transfasciatus* Miranda Ribeiro, 1908 ($IP = 41.49$), and the Loricariidae *Kronichthys heylandi* (Boulenger, 1900) ($IP = 20.30$). The third fish zone (FZ3) was represented by 5 sites between 100 and 263 m, and the species richness totaled 10. The Characidae family did not occur in FZ3, and the Heptapteridae *R. cf. transfasciatus* was the dominant species

($IP = 95.01$). The highest fish zone in the plateau (FZ4) was represented by the eight sites above 700 m. This low-relief region was dominated by the Gymnotidae *G. phantherinus* ($IP = 95.55$) whereas the other nine species were distributed in the families Cichlidae, Erythrinidae, Poeciliidae, Loricariidae, Crenuchidae, Trichomycteridae, and Characidae (Table 2). Between 300 and 700 m there is a high steeped region in the Serra do Mar mountain range that we defined as the third transition zone (TZ3). We did not sample at these reaches, but it is expected that their assemblages would be the poorest one, due to the high declivity and to the presence of several barriers to the fish movements (waterfalls and cascades), which prevents the colonization of most sites.

Discussion

Fish zones (FZ) can be thought as being relative homogeneous spatial units within the river basin, recognized by distinct patterns of assemblage structure and composition (Thorp et al., 2006; Welcomme et al., 2006). As for other riverine systems in tropical and temperate environments (Huet, 1959; Sheldon,

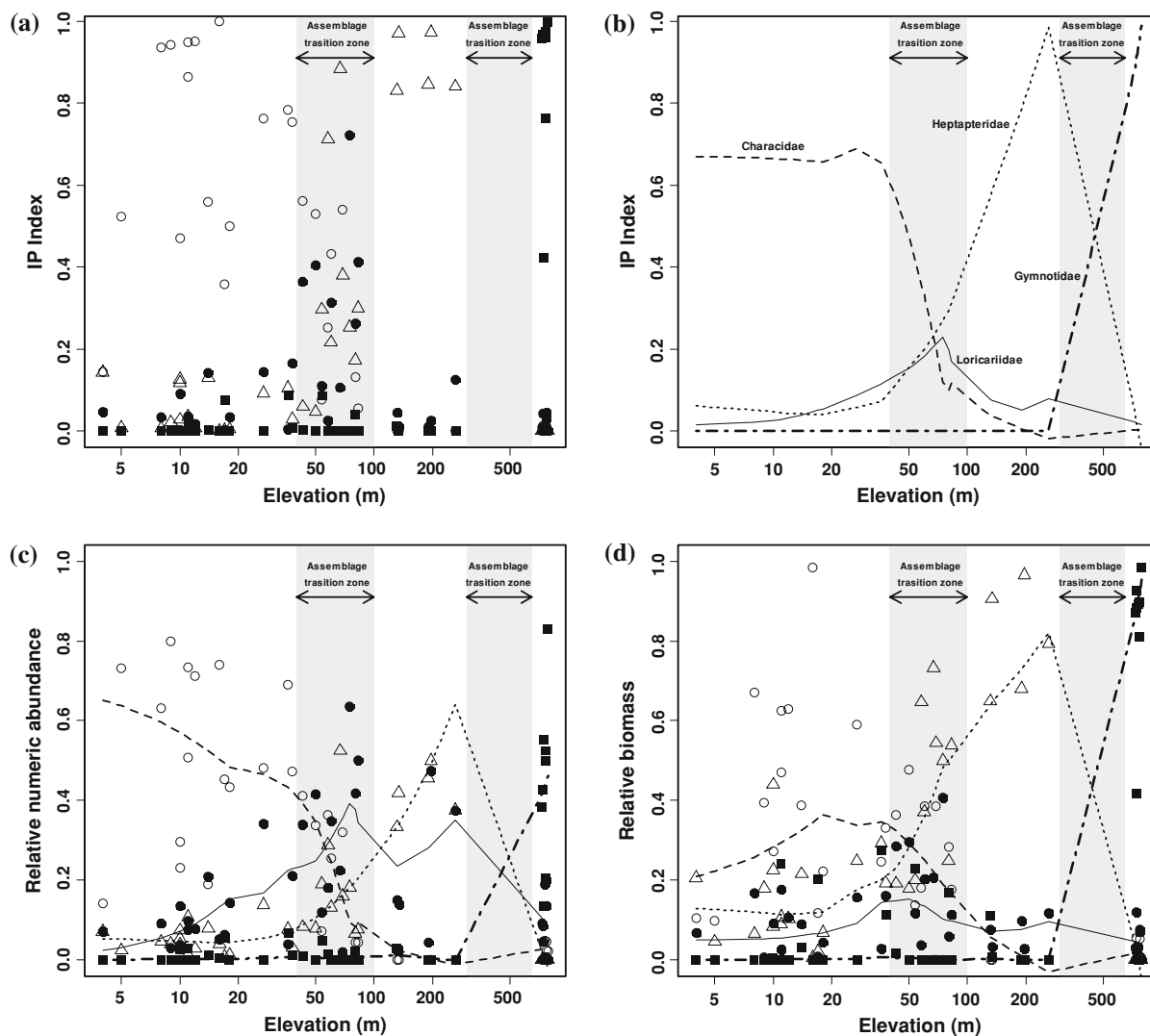


Fig. 3 **a** Scatterplot of the elevation versus *IP* index for Characidae (open circles), Heptapteridae (open triangles), Loricariidae (black circles), and Gymnotidae (black squares). **b** Smoothed lines from the LOWESS regression for the same data. The same patterns are showed for relative numeric abundance (**c**) and relative biomass (**d**). The two estuarine sites

in the Itanhaém river were excluded from the figures due to the absence or the low representativeness of these families. Elevation is in natural logarithmic scale. The proposal of the transition zones (sketched in gray) was based on the distribution and prevalence of these four dominant families along the elevation profile

1968; Winemiller & Leslie, 1992; Peres-Neto, 1995; Aarts & Nienhuis, 2003; Petry & Schulz, 2006; Lasne et al., 2007; Araújo et al., 2009; Orrego et al., 2009), we found evidences for longitudinal fish zonation in the Itanhaém river basin. The characterization of the proposed zones followed the pattern of dominance of different fish families. The fish zones represented the estuarine environment (FZ1, Ariidae dominant assemblages), the low-gradient rivers and streams in the coastal plain (FZ2, Characidae dominant

assemblages), the high steeped streams in the mountain range (FZ3, Heptapteridae dominant assemblages), and the low-gradient headwater streams in the plateau (FZ4, Gymnotidae dominant assemblages). Between two adjacent zones we found transition zones (TZ) where the assemblages had elements of the two adjacent FZ's (Tables 1, 2; Fig. 4). Our findings highlight a criticism to the earlier concept of fish zonation, i.e., that the zones are not discrete entities, but replace each other gradually

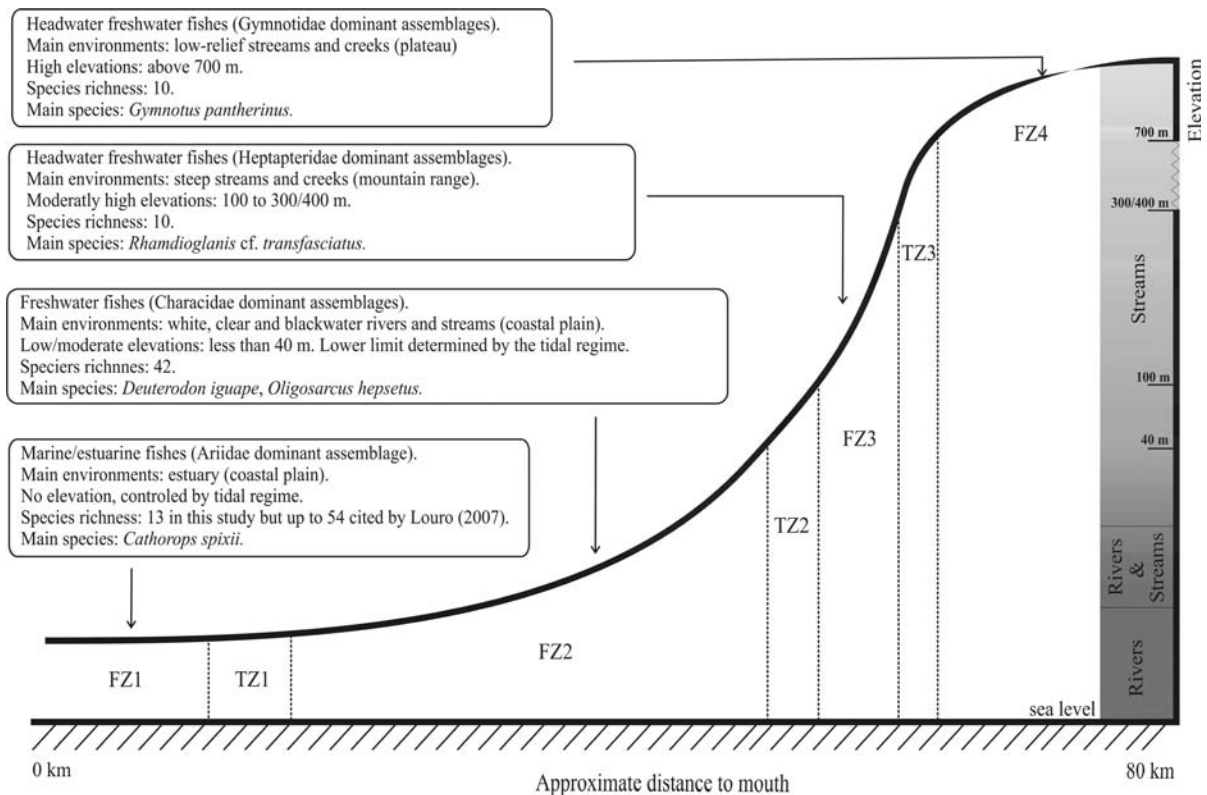


Fig. 4 Diagram of fish assemblage zonation in the Itanhaém river basin related to elevation. The distribution of the river and its streams along the elevation gradient (sketched in gray rectangle at right) was concerned to the 42 sampling sites, and not to the actual distribution of all these aquatic habitats in the basin. The highest river sampled was at 18 m (site 7), and the lowest stream at 8 m (site 34). The exact elevation limits for TZ1 varies with tidal regime. FZ1 estuary (Ariidae dominant

assemblages), TZ1 transition zone 1 (estuarine-freshwater assemblages dominated by the Sciaenidae *Bairdiella ronchus*), FZ2 fish zone 2 (Characidae dominant assemblages), TZ2 transition zone 2, FZ3 fish zone 3 (Heptapteridae dominant assemblages), TZ3 transition zone 3, FZ4 fish zone 4 (Gymnotidae dominant assemblages). The distances to the mouth are only approximated

along the downstream profile forming diffuse boundaries (Lasne et al., 2007). The FZ's and TZ's were organized according to the elevations sampled. In our case, elevation has a close relationship with different biogeographical region isolating the plateau from the mountain range and coastal plain fish faunas. Below 300 m, the elevation stressed the changes from rhithron to potamon areas in the freshwater sites. The elevation criterion could not be used for the lower zones (FZ1 and TZ1) because their elevation varied with the tidal regime. Thus, the limits between these zones were defined according to the contribution of the marine/estuarine fishes in the samples, which in turn depends on the proximity of the basin mouth.

The patterns of species addition and replacement are commonly described for lotic gradients (Peres-Neto, 1995). Species addition seems to prevail in less

abrupt transitions whereas species substitution resulted from abrupt transitions along the fresh/salt water interface or between distinct geomorphic formations, and are expressed by higher rates of species turnover (Balon & Stewart, 1983; Winemiller & Leslie, 1992; Edds, 1993; Wilkison & Edds, 2001). In the Itanhaém river basin, we detect higher species turnover between FZ4 and FZ3 representing the geomorphic transition from the high steeped streams in the mountain range to the low-gradient streams in the plateau. Some fishes caught in FZ4, such as *Glandulocauda melanogenys* Eigenmann, 1911 and *Pseudotocinclus cf. tietensis* (R. Ihering, 1907), are typical representatives of the adjacent upper Tietê basin. On the other hand, *G. pantherinus* evolved first in coastal drainages and irradiated to adjacent interior basins only recently (Ribeiro, 2006). *G. pantherinus*

was highly associated to sandy streams, and similar to other Gymnotidae species, it has elongated body shape with the caudal fin absent. During the day, it lives along the marginal vegetation, but at night, it explores the environment to feed on insects and eventually on small fishes (Oyakawa et al., 2006). The complex and recent history of faunal interchange between the upper Tietê basin and adjacent coastal areas are examples of recent vicariant events that took place during the Tertiary and can be explained by the occurrence of tectonic movements and erosive retreats of the Serra do Mar (Ribeiro, 2006; Ribeiro et al., 2006). Therefore, some headwaters that otherwise run to interior watersheds, now run to coastal drainages, causing truly hybrid zones affecting the distribution and the evolutionary patterns of several groups. For instance, Takako et al. (2005) described morphological differences among species of the genus *Parotocinclus* caught in the upper Tietê and in the coastal drainages of São Paulo State. The other abrupt transition zone was TZ1, representing the change between fresh and salt water environments. Although the freshwater fishes in TZ1 prevail in species number, they accounted for less than 10% of the total importance (Table 2). The dominant species, *B. ronchus*, is essentially carnivorous, feeding on several benthic organisms, and uses the more internal estuarine areas, where it remains for most of its life cycle (Louro, 2007). In general, this species is not caught in deeper marine waters in the littoral of São Paulo State (Souza et al., 2008). The abundance of *B. ronchus* in the internal area of the Itanhaém estuary was already detected by Silva Jr. & Petrere Jr. (1994). The freshwater fishes in TZ1 were caught mainly in sites 3 and 4 (mouth of the rivers Preto and Branco, respectively). Leung & Camargo (2005) sampled the fishes associated to aquatic macrophyte stands in the Branco river (12 km to the Itanhaém river mouth and next to our site 3) and, although they used different sampling procedures, the results were quite similar to ours, with the dominance of freshwater fishes (150 individuals and 14 species), and a lower contribution of marine/estuarine species (8 individuals and 5 species). In site 2 (upper Itanhaém channel), the freshwater species were caught only in the summer season (wet season). This suggests temporal patterns in species turnover in the estuary, which might be mediated by seasonal variations in the salinity levels (Silva Jr. & Petrere Jr., 1994;

Barletta et al., 2005; Louro, 2007). In the estuaries of the Estação Ecológica da Juréia (South littoral of the State of São Paulo) the genus *Centropomus* is more frequently caught between March and April, indicating seasonal shifts in this species requirements which may be related to reproductive or feeding behavior (Sabino & Silva, 2004). The two species of *Centropomus* (*C. parallelus* and *C. undecimalis*) caught in Itanhaém river basin occurred from FZ1 to FZ2. These fishes are active, visually oriented carnivores, and may exert influence upon freshwater and estuarine fish assemblages through predation (Leung & Camargo, 2005). Owing to their migratory habits, from estuary to freshwaters zones, they are probably susceptible to river damming in coastal basins. The less abrupt transitions detected in TZ2 were marked by species addition downstream and by a gradual change in the dominant families. This gradual change can be verified in the Fig. 2, which shows the higher contributions of Heptapteridae between 100 and 300 m, and of Characidae below 40 m. Loricariidae shows a modal distribution in TZ2 between 40 and 100 m. Petry and Schulz (2006) detected the dominance of Characidae and Loricariidae species for a subtropical Brazilian river but a lower contribution of Heptapteridae. This trend probably reflects the fact that these authors sampled at elevations below 160 m, downstream to river barriers such as cascades or waterfalls. Deus (1999) found marked differences in the composition of the stream fish assemblages above and below waterfalls in the Estação Ecológica da Juréia.

The Characidae comprise the most numerous and diverse freshwater family in Central and South America. A large number of Characidae species were recently rearranged under *Incertae Sedis* genera due to uncertainties about their phylogenetic relationships. This is the case for *D. iguape* and *O. hepsetus*, the dominant species in FZ2. Only the few groups for which there is evidence of monophyly were maintained in their traditional subfamilies (Malabarba et al., 1998; Reis et al., 2003). The high heterogeneous nature of Characidae is exemplified by the diversity of reproductive behaviors and feeding habits. In the coastal basins, some species have internal insemination (genera *Hollandichthys*, *Mimagoniates*, and *Glandulocauda*), an uncommon behavior that protects the sperm cells from the acid waters (Menezes et al., 2007). Other species of forested

streams present short longitudinal movements related to reproductive strategies, with the adults migrating upstream to spawn during prolonged periods (Mazzoni et al., 2004). Long reproductive periods are common for some species of Characidae in the headwaters of the Atlantic rain forest (Mazzoni et al., 2005; Souza, 2009). Concerning the diversity of feeding habits, several species known as “lambaris” are omnivorous, insectivorous, or herbivorous. The species of the genus *Deuterodon*, for example, were classified as omnivorous (Mazzoni & Resende, 2003) or herbivorous (Esteves and Lobón-Cervia, 2001) depending on the author. One of the first dietary studies classified *D. iguape* as omnivorous but highlighted the high presence of algae in the stomachs and ontogenetic changes, with juveniles feeding highly on insects (Sabino & Castro, 1990). The capacity to change the feeding behavior according to different ontogenetic stages or due to differences in resource availability is common to several tropical freshwater fishes (Agostinho et al., 2007). In the Itanhaém river basin, as in other coastal drainages of southeast Brazil, the only piscivorous Characidae was *O. hepsetus*. However, the diet of *Oligosarcus* is not restricted to fishes, but also includes other animals such as insects (Casatti, 2002). The piscivory in this case may be related to the pattern of individual growth, where larger individuals can feed on larger items. Considering the diversity of habits hitherto cited, perhaps, the only common feature for the Characidae family as a whole would be the laterally compressed body which favors nektonic habits and the maneuverability in low current conditions (Petty & Schulz, 2006).

The Heptapteridae are commonly represented by carnivorous catfishes that feed on a variety of items such as insects (adults or larvae), crustaceans, or small fishes, while the Loricariidae feed basically on periphyton, and eventually on small benthonic insects (Gerhard, 1999; Casatti, 2002; Oyakawa et al., 2006; Menezes et al., 2007; Braga et al., 2008). These two families have dorsally compressed bodies and have nektobenthic or benthic habitats (Langeani et al., 2005) which favor the colonization of fast flowing and steep environments, such as the streams of TZ2 and FZ3. We hypothesized that the gradual change from Characidae to Heptapteridae, and the distribution range of Loricariidae probably resulted from complex interactions between flow suitability and the

amount of food resources available for the fish assemblages. In small headwater creeks such as those in FZ3, the riparian vegetation may prevent the extensive growth of the periphyton, and the trophic food web may be sustained by the input of allochthonous insects (Barrella et al., 2000).

Implications of fish zonation

The delimitation of fish zones has theoretical applicability for community ecology, and their recognition could help to understand the regulatory mechanisms underlying assemblage dynamics. Models of the strength and frequency of species interactions, for example, stated that abundant species have strong effects on rare species (Vázquez et al., 2007). The most abundant species are supposed to play a pivotal role in the determination of patterns of biotic interactions in ecological networks. Flecker (1992) detected indirect influences of fish on the abundance of invertebrates in Andean streams, an effect that increases with fish density, and which were mediated by the modification in the resource distribution used by these invertebrates. For tropical streams, Gilliam et al. (1993) described complementary distribution of predator (*Hoplias*) and prey (*Rivulus*) species and significant effects of interspecific competition in which the presence of *Poecilia* depressed the growth rate of *Rivulus*. On the other hand, such biotic interactions can be difficult to verify without non-manipulated experiments. Indeed, in systems subjected to stochastic environmental fluctuations, their potential to maintain the assemblage dynamics can be minimum (Jackson et al., 2001). Even in that case, we could expect that the dominant groups in specific locations are those that better explore the amount of available resources. Concerning the complexity behind these patterns, we propose that the FZ's (and TZ's) might be used as baseline for testing ecological theories of community assembly along the longitudinal gradient of these environments.

Applied issues related to delimitation of fish zones are usually directed to the development of ecological indicators that could be used for the rehabilitation of degraded areas (Karr, 1999; Aarts & Nienhuis, 2003; Welcomme et al., 2006; Lasne et al., 2007; Orrego et al., 2009; Araújo et al., 2009). Other attempts to develop arrangements of fish zonation used more complex methods to define the indicator species (Petty

& Schulz, 2006; Lasne et al., 2007), but we prefer to consider the representativeness of higher taxonomic levels (families) to provide a valuable comparisons with other systems in the Brazilian coast. Indeed, by using the most abundant groups to define the fish and transition zones, we expected that they can be used as sentinel groups (Noble et al., 2007) to detect non-natural modification in the river ecosystems that might occur in the near future due to river damming, water abstraction, deforestation, or water pollution. Fish-based methods to detect the ecological integrity of aquatic systems are well advanced in Europe and United States (USEPA, 2002, 2006, 2007; Cowx & Schramm, 2007), while in Brazil, these models are in their infancy (Araújo, 1998; Moraes & Molander, 1999; Araújo et al., 2003, 2009; Casatti, 2004; Bozzetti & Schulz, 2004; Ferreira & Casatti, 2006; Petesse et al., 2007; Casatti et al., 2009). Thus, the evaluation of areas with low levels of disturbance at the watershed scale in ecoregions with high endemism and next to metropolitan centers is valuable to define reference conditions for the conservation of running waters in the country (Metzger & Casatti, 2006; Lasne et al., 2007).

The position preferentially occupied by the fishes is commonly considered in indices of biotic integrity to detect changes in the flow characteristics and in the substrate composition resulting from siltation or channel ratification (Karr, 1981). The use of other relevant metrics for the classification of functional guilds, such as feeding guilds, depends on analyzes of stomach contents and behavioral studies. Casatti et al. (2001) and Casatti (2002) provided information about the feeding guilds co-occurring in streams of the Parque Estadual do Morro do Diabo (high Paraná River basin). Besides the division in carnivorous, periphytivor, and omnivorous fishes, the feeding guilds were sub-divided according to the alimentary strategies, the periods of activity, and the use of different micro-habitats, which truly defines how these fishes may affect the stream ecosystem. Except for local particularities, this classification is quite similar to the definition of functional groups used for temperate regions (Higgins & Strauss, 2008). The species studied by Casatti et al. (2001) and Casatti (2002) were different from those caught in the present study (mainly because the different basin systems) but some genera and families were the same. For example, the genera of the three predator fishes

described by the authors (*Oligosarcus*, *Hoplias*, and *Crenicichla*) are common to Itanhaém river (Table 2). The two Heptapteridae species, *Imparfinis mirini* Haseman, 1911 and *Phenacorhamdia hohenei* (Miranda Ribeiro, 1914) had occasional occurrence, but similar to the other catfishes (*Trichomycterus* and *Corydoras*), they were classified as benthonic species that revolve the substrate using different tactic, micro-habitats, or active periods. The Loricariidae were all periphytivor but differed in the activity period and micro-habitat use, whereas the “lambaris” (family Characidae and genera *Astyanax* and *Moenkhausia*) feed during the day in the water column. These characteristics highlighted by Casatti et al. (2001) and Casatti (2002) are related to common metrics used in the formulation of the IBI indices in Brazilian streams, being the Characidae, in general, classified as “water column” or “nektonic” species while the Heptapteridae and Loricariidae are classified as a “benthic” group (Bozzetti & Schulz, 2004; Casatti et al., 2009).

Considering the main riverine habitats along the longitudinal gradient in the Itanhaém river basin, the estuary (represented by FZ1 and the lower part of TZ1) is composed by the short and shallow Itanhaém river channel. There are no coastal lagoons, and the few side arms and tributaries are urbanized and/or polluted (Souza-Pereira & Camargo, 2004). The freshwater lowland rivers are represented by the meandering main channels of FZ2. The 4th order stretches of the rivers Branco and Mambu are constrained channels with medium/high lateral banks that prevent extensive lateral inundation. The fifth-order stretches can be classified as unconstrained channels, seasonally subjected to lateral inundation. The restinga forest in the Preto microbasin, for example, is constantly flooded in the wet season between December and March. In the Aguapeu microbasin the original restinga was removed, and the region is now highly urbanized. TZ2 and FZ3 can be classified as rhithron zones, where prevail constrained and steep stream channels. The low-gradient headwaters in FZ4 are of special interest to develop ecological indicators because its ichthyofauna is common to several other isolated drainages on the plateau (Takako et al., 2005; Ribeiro et al., 2006; Serra et al., 2007; Menezes et al., 2007). The appeal for rehabilitation studies in this zone is reinforced by its closeness to well-developed metropolitan areas

and by the pristine conditions of most sites. It is part of the last preserved region of Atlantic Forest around the metropolitan area of the São Paulo city.

The high endemism at species levels in the coastal basins prevents the use of this taxonomic status as broad comparative criterion among the isolated drainages. Thus, considering that all the dominant fish families described here are widespread, at least in the coastal basins of the Brazilian southeast (Oyakawa et al., 2006; Menezes et al., 2007), we provided information on family levels in an attempt to grouping species with similar behavior, feeding habits, and morphology (Karr, 1981). The pattern of high steep gradients throughout short distances is common to the coastal basins in the Serra do Mar between the States of Rio de Janeiro and Santa Catarina, but we anticipate that the length of the FZ's will vary among different coastal basins depending on the general hidrography design and the elevation profile. We defined the FZ's according to elevation, but better measures could be steepness and the presence of downstream barriers, combined with some hydrologic index. As an example, Lamouroux et al. (2002) used an index called "Froude number" (FR) to describe the stream hydraulics which includes water velocity and depth. FR was a good descriptor for intercontinental fish traits related to physical stress in streams. For European rivers, Lasne et al. (2007) found that slope (and not elevation or river order), air temperature (as surrogate of water temperature), mean width and mean depth were the most influential factors that separate the clusters grouping of several indicator species. Next to the estuary, the distance to the Itanhaém river mouth or measures of the salinity levels could be more directly related to the FZ's (Leung & Camargo, 2005). Finally, we argue that an extensive evaluation of other coastal drainages at Brazilian Southeast is necessary. This will allow the verification of repeatable patterns of assemblage organization, and the classification of functional groups based on their ecological requirements will certainly enhance the theoretical and applied researches in these poorly known but threatened basins.

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